



Morphology and biology of *Polydora hoplura* Claparède, 1868 (Annelida: Spionidae)

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Abstract

Polydora hoplura Claparède, 1868 is one of the largest species among congeners, attaining 6 cm in length and 2 mm in width for more than 200 chaetigers. It is a harmful shell-borer unintentionally transported with objects of aquaculture across the world. Brief original description and absence of type material resulted in confusion with the identification of this species. Herein, we review previous records, establish a neotype and redescribe *P. hoplura* based on newly collected material from the type locality, the Gulf of Naples. We also describe worms from other localities in Italy, illustrate adult morphology and report gradual development of taxonomic features of this species in ontogenesis based on material from South Korea.

Key words: polychaete, taxonomy, bioinvasion, shell-borer, oyster, abalone

Introduction

The spionid polychaete *Polydora hoplura* was originally described as a borer in barnacle shells in the Gulf of Naples, Tyrrhenian Sea, Italy, by Claparède (1868). The species was also found in barnacles in the Gulf of Marseille, France (Marion & Bobretzky 1875) and soon thereafter was reported as a common borer in oysters and other mollusks in France (Giard 1881; Saint-Joseph 1894; Soulier 1903; Douvillé 1907; Fauvel 1927; Dollfus 1932; Lamy & André 1937; Cornet & Rullier 1951; Lejart & Hily 2011), Italy (Carazzi 1893; Lo Bianco 1893; Graeffe 1905; Fresi *et al.* 1983; Colognola *et al.* 1984; Solis-Weiss *et al.* 2004; Castelli *et al.* 2008), British Islands (McIntosh 1909, 1915a, b, 1923; Wilson 1928; Clavier 1989), Spain (Rioja 1917a, 1931; Aguirrezabalaga 1984; Acero & San Martín 1986; Parapar *et al.* 2009), Netherlands (Korringa 1951), Montenegro and Croatia (Graeffe 1905; Požar 1972; Stjepčević 1974; Igić 1982; Labura & Hrs-Brenko 1990; Požar-Domac 1978, 1994; Mikac 2015), Portugal (Amoureux & Calvário 1981; Vasconcelos *et al.* 2007), Greece (Simbora & Nicolaidou 2001; Karalis *et al.* 2003), and Belgium (Zintzen & Massin 2010). Outside Europe, *P. hoplura* was reported boring in soft limestone, sandstone, and shells of oysters, abalone and other mollusks in South Africa (Day 1955, 1967; Nel *et al.* 1996; Simon *et al.* 2006, 2010; Simon & Booth 2007; Boonzaaier *et al.* 2014; David *et al.* 2014; Williams *et al.* 2016), Kuwait (Mohammad 1971), New Zealand (Read 1975; Handley 1995; Handley & Bergquist 1997), Australia and Tasmania (Blake & Kudenov 1978; Hutchings & Turvey 1984; Leonart 2001; Leonart *et al.* 2003), Tunisia (Ayari *et al.* 2009), the Aegean coast of Turkey (Çinar & Dagli 2013), São Paulo, Brazil, and California, USA (Radashevsky & Migotto 2016). It was reported as one of the most serious pests causing damage to cultivated oysters and abalone in South Africa (Nel *et al.* 1996; Simon *et al.* 2006, 2010; Simon & Booth 2007) and mortality of abalone cultivated in Tasmania (Leonart 2001; Leonart *et al.* 2003). As *Polydora uncinata* Sato-Okoshi, 1998

(see Radashevsky & Migotto 2016; Sato-Okoshi *et al.* 2016), it was reported from Japan (Sato-Okoshi 1998, 1999), Chile (Radashevsky & Olivares 2005), South Korea (Sato-Okoshi *et al.* 2012), and Western Australia (Sato-Okoshi & Abe 2012) (Fig. 1).

Polydora hoplura is one of the largest species among congeners, attaining 6 cm in length and 2 mm in width for more than 200 chaetigers (Carazzi 1893; Lo Bianco 1893). It is also one of the most destructive shell-borers, considered a pest negatively affecting oyster and abalone culture (Simon & Sato-Okoshi 2015).

The brief original description and the absence of type material have resulted in confusion with the identification of this species. Herein, we establish a neotype and redescribe *P. hoplura* based on newly collected material from the type locality, the Gulf of Naples. We also describe worms from other localities in Italy, illustrate adult morphology and report gradual development of taxonomic features of this species in ontogenesis based on material from South Korea.

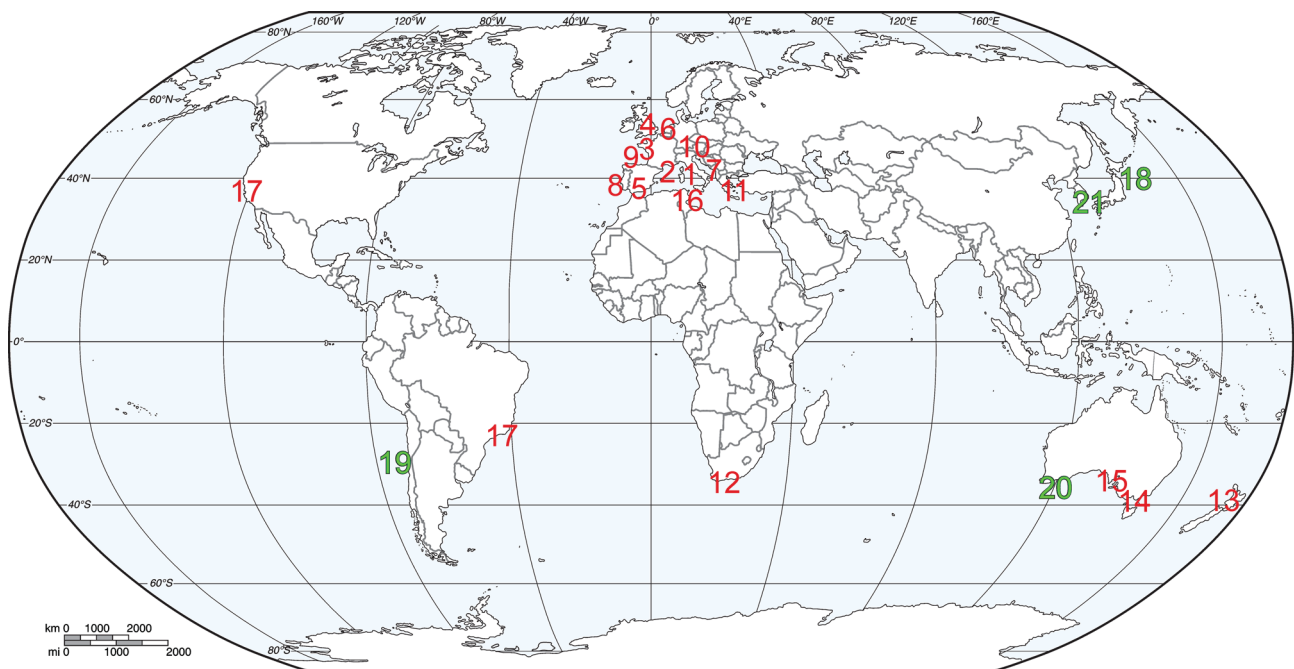


FIGURE 1. Map showing world-wide records of *Polydora hoplura* and collecting sites reported in the present study (red numbers). 1—Italy (Claparède 1868; Carazzi 1893; Lo Bianco 1893, 1909, Fresi *et al.* 1983; Colognola *et al.* 1984). 2—Mediterranean France (Marion & Bobretzky 1875; Soulier 1903). 3—Atlantic France (Giard 1881, Saint-Joseph 1894; Douvillé 1907; Dollfus 1921, 1932; Cornet & Rullier 1951; Lejart & Hily 2011). 4—British Islands (McIntosh 1909, 1915, 1923; Wilson 1928; Clavier 1989). 5—Mediterranean Spain (Rioja 1931; Acero & San Martín 1986). 6—Netherlands (Korringa 1951), Belgium (Zintzen & Massin 2010). 7—Montenegro (Stjepčević 1974). 8—Portugal (Amoureux & Calvário 1981, Vasconcelos *et al.* 2007). 9—Atlantic Spain (Aguirrezabalaga 1984; Parapar *et al.* 2009). 10—Croatia (Labura & Hrs-Brenko 1990), Italy (Solis-Weiss *et al.* 2004). 11—Greece (Simboura & Nicolaidou 2001; Karalis *et al.* 2003), Turkey (Çinar & Dagli 2013). 12—South Africa (Day 1967; Nel *et al.* 1996, Simon *et al.* 2006, 2010, Simon & Booth 2007). 13—New Zealand (Read 1975; Handley 1995; Handley & Bergquist 1997). 14—Australia and Tasmania (Blake & Kudenov 1978; Lleonart 2001; Lleonart *et al.* 2003). 15—Australia (Hutchings & Turvey 1984). 16—Tunisia (Ayari *et al.* 2009). 17—São Paulo, Brazil, and California, USA (Radashevsky & Migotto 2016). Records of *Polydora uncinata* (green numbers): 18—Sato-Okoshi 1998, 1999. 19—Radashevsky & Olivares 2005. 20—Sato-Okoshi *et al.* 2008. 21—Sato-Okoshi *et al.* 2012.

Material and methods

Field collections were made in France and Italy in June–July 2014 and in South Korea in 2013–2016. We collected gastropods, bivalves, barnacles and coralline algae manually in the intertidal zone and in cultivation farms, and also collected samples with grabs on board research vessels. Polychaetes were removed after cracking infested shells with a hammer and pliers, relaxed in isotonic magnesium chloride and examined alive under light microscopes in the laboratory. We photographed live relaxed individuals using microscopes equipped with digital cameras. Final

plates were prepared using CorelDRAW®X5 software. After examination, we fixed worms in 10% formalin solution, rinsed in fresh water and transferred to 70% ethanol. Fixed specimens are deposited in the polychaete collection of the Museum of the A.V. Zhirmunsky Institute of Marine Biology (MIMB), Vladivostok, Russia, the Senckenberg Museum (SMF), Frankfurt am Main, Germany, and in the Library of Marine Samples of the Korea Institute of Ocean Science and Technology (KIOST), Jangmok, South Korea. Complete information about samples is provided below, in the *Material* section of the *Results*, along with the description of specimens. The number of specimens in a sample is given in parentheses after the museum abbreviation and registration number.

Results

Polydora hoplura Claparède, 1868

(Figs 2–4)

Polydora hoplura Claparède, 1868: 318–319, pl. XXII, fig. 2; 1869: 58–59, pl. XXII, fig. 2; 1870: 58–59, pl. XXII, fig. 2. Marion & Bobretzky 1875: 84. Carazzi 1893: 20–21, pl. 2, figs 6, 7, 13, 16, 18. Lo Bianco 1893: 30; 1909: 584. Saint-Joseph 1894: 65. Soulier 1903: 83–86, fig. 12. Douvillé 1907: 364–365, fig. 7. McIntosh 1909: 173–174; 1915a: 212–213; 1915b: pl. 101: fig. 10, pl. 106: fig. 6; 1923: 486–487. Fauvel 1927: 50, fig. 17a–g. Wilson 1928: 578–585, textfig. 2, pls V–VII (larval morphology). Read 1975: 411–412, fig. 6. Blake & Kudenov 1978: 264, fig. 47. Hutchings & Turvey 1984: 15. Colognola *et al.* 1984: 748. Leonart 2001: figs 4–6, 9, 26–32. David *et al.* 2014: figs 4–6 (larval morphology). Radashevsky & Migotto 2016: 2–7, figs 2–5 (adult and larval morphology). Sato-Okoshi *et al.* 2016: 3–6, figs 6, 7. *Polydora (Polydora) hoplura*: Rioja 1931 (*Part.*): 70, pl. 19, figs 8–13. Hartmann-Schröder 1971: 305; 1996: 318. *Polydora hoplura hoplura*: Day 1967: 468, fig. 18.2k–m. *Leucodora sanguinea* Giard, 1881: 71–73. *Fide* Dollfus 1921: 17; 1932: 275. *Polydora uncinata* Sato-Okoshi, 1998: pp. 278–280, fig. 1; 1999: p. 835. Radashevsky & Olivares 2005: 491–494, figs 2–4. Sato-Okoshi *et al.* 2008: 493–495, figs 2–3; 2012: 87, figs 4A–B, D. Sato-Okoshi & Abe 2012: 43–44, fig. 3. *Fide* Radashevsky & Migotto 2016: 2; Sato-Okoshi *et al.* 2016: 4.

Material. **Italy**, Tyrrhenian Sea, **Campania**, Gulf of Naples, Port of Ischia, Ischia Is., 40.74439°N, 13.93948°E, intertidal, Radashevsky, V.I. & M.C. Gambi, 07 Jul 2014: from shell of live whelk *Stramonita haemastoma* (Linnaeus, 1767), SMF 24359 (**neotype**), two individuals from shells of live whelk *S. haemastoma* and two individuals from shell of live European flat oyster *Ostrea edulis* Linnaeus, 1758, MIMB 28148 (4). Tyrrhenian Sea, **Lazio**, Fiumicino, 41.7739°N, 12.2189°E, from a shell in fouling of artificial platform, st. 5, 5 m, spring 1979, Gambi, M.C., MIMB 33027 (34), 33028 (7). Ionian Sea, **Apulia**, Taranto, 40.4323°N, 17.2409°E, 1 m, from shells of the oyster *O. edulis*, Radashevsky, V.I., 15 Jul 2014, MIMB 33029 (23).

France, **Brittany**, La Manche, NE to Roscoff, 48.7487°N, 3.9062°W, 40 m, from empty scallop shell, Radashevsky, V.I. & C. Houbin, 27 May 2014, MIMB 33030 (1). **Aquitaine**, Bay of Biscay, Arcachon Bay: Jacquets, 44.7212°N, 1.1887°W, from shells of Pacific oyster *Crassostrea gigas* (Thunberg, 1793), Radashevsky, V.I. & S. Gasmi, 12 Jun 2014, MIMB 33031 (22); la Chapelle, 44.6645°N, 1.1802°W, 9 m, from shells of Pacific oyster *C. gigas*, Radashevsky, V.I. & B. Gouillieux, 13 Jun 2014, MIMB 33032 (25). Legallais, Arcachon, 44.663914°N, 1.175977°W, rocky intertidal, from shell of gastropod *Ocenebra erinaceus* (Linnaeus, 1758) occupied by hermit crab *Clibanarius erythropus* (Latreille, 1818), Lavesque, N., 16 Nov 2016, MIMB 33064 (3). **Languedoc-Roussillon**, Gulf of Lion, Leucate, 42.8778°N, 3.0229°E, 2 m, from shells of the Pacific oyster *C. gigas*, Radashevsky, V.I. & C. Labrune, 26 Jun 2014, MIMB 33033 (19).

South Korea, East China Sea, **Jeollanam-do Province**, Wando County, from shells of abalone *Haliotis discus hannai* Ino, 1953 cultivated in cages: Sinji Is., 34.345°N, 126.886°E, 30 Mar 2005, MIMB 33034 (7); Bogil Is., 34.1825°N, 126.5314°E, 7 May 2013, MIMB 33035 (8); Keumil Is., 34.4611°N, 127.0275°E, 27 May 2013, MIMB 33036 (30); Nohwa Is., 34.226117°N, 126.425833°E, 07 May 2013, MIMB 33037 (17); Seohwa Is., 34.317°N, 126.5075°E, 20 Nov 2013, MIMB 33038 (17); 34.191°N, 126.635°E, 27 Nov 2013, MIMB 33039 (13); Soan Is., 34.191°N, 126.635°E, 14 Jun 2016, MIMB 33057 (8). Yecheon County, Yeosu, 34.6344°N, 127.6408°E, from shells of abalone cultivated in land-based tanks, 12 Nov 2013, MIMB 33040 (2). **Gyeongsangnam-do Province**, Geoje Is., from shells of cultivated Pacific oyster *C. gigas*: 34.82°N, 128.5°E, 22 Oct 2013, MIMB 33041 (4); 34.97°N, 128.62°E, 31 May 2016, MIMB 33056 (7). **Jeju Province**, Jeju Is., from shells of abalone *H. discus hannai* cultivated in land-based tanks: 33.472252°N, 126.912332°E, 23 May 2013, KIOST BSMA 2 (15),

MIMB 28076 (120+). Cheongjeonghae Fisheries, 33.356012°N, 126.182154°E, 28 Aug 2013, MIMB 33042 (13). Dongjin Fisheries, 33.435425°N, 126.266602°E, 28 Nov 2013, KIOST BSMA 12 (7), MIMB 33043 (12); 28 Mar 2014, MIMB 33048 (20+); 30 Apr 2014, MIMB 33049 (10+); 30 May 2014, MIMB 33050 (20+). Halla Abalone, 33.470857°N, 126.917034°E, 28 Nov 2013, KIOST BSMA 13 (16), MIMB 33044 (15); 27 Mar 2014, MIMB 33047 (6+). Jaeil Fisheries, 33.469882°N, 126.918601°E, 28 Nov 2013, KIOST BSMA 14 (16), MIMB 33045 (100+); 3 Jun 2014, KIOST BSMA 6952 (50+), MIMB 33046 (100+).

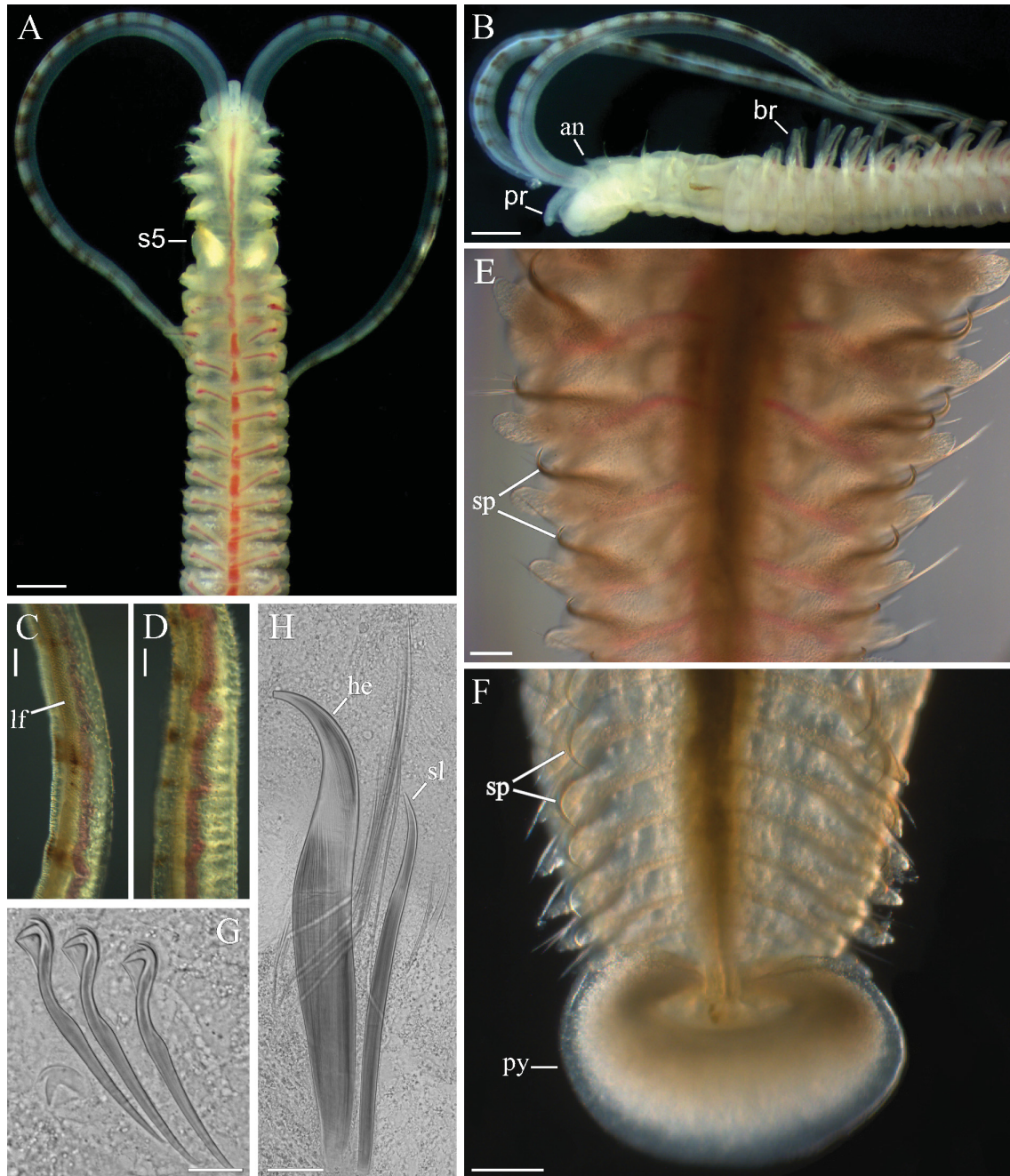


FIGURE 2. Adult morphology of *Polydora hoplura* (Wando, South Korea. MIMB 33035). A, anterior end, dorsal view, showing black bands on palps. B, same, left lateral view, showing short occipital antenna on the prostomium. C, distal fragment of palp, with fronto-lateral rows of short papillae with non-motile cilia on top arranged along frontal groove. D, basal fragment of palp, with short papillae with non-motile cilia on top sparsely scattered on abfrontal surface. E, posterior chaetigers with heavy recurved spines in notopodia, dorsal view. F, posterior end, showing cup-shaped pygidium with middorsal gap, dorsal view. G, bidentate hooded hooks from a middle neuropodium. H, spines and slender capillaries from a posterior notopodium. *an*—occipital antenna; *br*—branchiae; *he*—heavy sickle-shaped spine; *lf*—latero-frontal papillae with non-motile cilia; *pr*—prostomium; *py*—pygidium; *sl*—slender awl-like spine; *sp*—heavy spines in notopodia; *s5*—modified chaetiger 5 with heavy falcate spines in notopodia. Scale bars: A, B = 500 μ m; C–F = 200 μ m; G, H = 50 μ m.

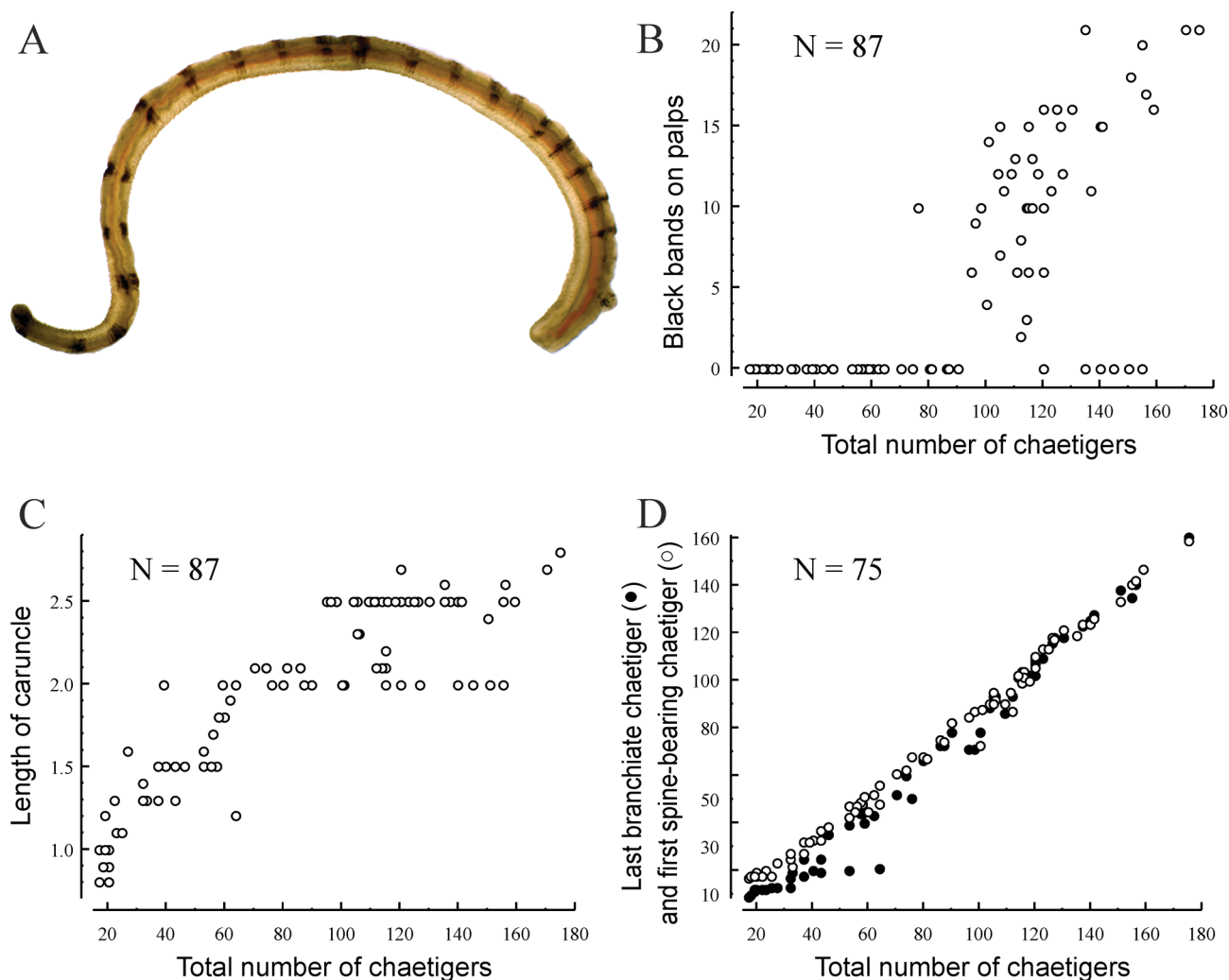


FIGURE 3. Adult morphology of *Polydora hoplura* (South Korea). A, palp with regularly arranged black paired bands. B, relationships between number of black bands on palp and total number of chaetigers in worm. C, relationships between length of caruncle (in chaetiger numbers) and total number of chaetigers in worm. D, relationships between arrangement of branchiae (referring to number of the last branchiate chaetiger), arrangement of spines in posterior notopodia (referring to number of the first spine-bearing chaetiger) and total number of chaetigers in worm.

Adult morphology (Material from the type locality, Gulf of Naples, Italy). Neotype (SMF 24359) largest complete individual 30 mm long, 1.5 mm wide with 175 chaetigers; other individuals (MIMB 28148) 8 to 11 mm long, with 60 to 100 chaetigers. Pigmentation absent on body. No pigment on palps in a 60-chaetiger individual, and in an individual 11 mm long with 100 chaetigers; 75-chaetiger individual and neotype with five and seven paired black bands on each palp, respectively. Prostomium anteriorly incised, extending posteriorly to end of chaetiger 3 as a low caruncle. Occipital antenna absent in 60- and 75-chaetiger individuals; larger individuals, including neotype, with short occipital antenna on prostomium. Eyes absent in neotype; up to four eyes present or eyes absent in other individuals. Chaetiger 1 with short capillaries only in neuropodia. Chaetiger 5 with up to four dorsal superior winged capillaries, six heavy falcate spines alternating with bilimbate-tipped companion chaetae, and six ventral winged capillaries; falcate spines with lateral flange. Hooded hooks in neuropodia from chaetiger 7, up to ten in a series, not accompanied by capillaries; hooks bidentate, with constriction on shaft. Posterior notopodia (from chaetiger 155 onwards in a 175-chaetiger neotype) each with 1–2 heavy recurved spines and a tuft of slender capillaries; spines with curved tips directed medially. Branchiae from chaetiger 7 continuing posteriorly along most of body (on chaetigers 7–154 in neotype). Pygidium white, cup-shaped with dorsal gap. Of five individuals, two were females (175-chaetiger neotype with oocytes in chaetigers 40–113), two had no gametes, and one was male (10 mm long with 75 chaetigers, with branchiae on chaetigers 7–39, and nototrochs composed of single rows of cilia) with spermatocytes, tetrads of spermatids and individual spermatozoa (introsperm with elongated head and midpiece, similar to those in other *Polydora* species) floating in coelom in chaetigers 29–44.

Other material from Italy and France. Large worms of a size range similar to specimens from type locality (see above). Black pigment diffused on anterior part of prostomium (in front of eyes) in some individuals, varying from weak only on lateral sides to intense on lateral and dorsal sides of prostomium. Similar pigment of variable intensity diffused on dorso-lateral sides of peristomium in some individuals. Up to ten black paired bands present on each palp and black pigment diffused on pygidium in some individuals. Notopodia of 5–16 posterior chaetigers with heavy recurved spines in addition to capillaries. Pygidium flaring disc with wide dorsal gap.

Material from South Korea (*Polydora hoplura* in Korean galgori-kin-eolgool-gat-ji-rung-i, meaning a long face worm with hook). Up to 55 mm long and 2 mm wide for 180 chaetigers. Body pale to light tan in life; with numerous glandular cells on dorsal side from chaetigers 10–15 giving dorsum whitish appearance (Fig. 2A). Remains of larval melanophores present on dorso-lateral sides of 15–16 anterior chaetigers in individuals up to 50–60-chaetiger stage; larger worms usually lacking black pigment on body. Black narrow longitudinal stripes on lateral sides of anterior part of prostomium and a pair of small black patches on dorsal side of peristomium present in three individuals (of more than one thousand examined). Up to 25 black paired bands present on each palp in individuals with more than 50 chaetigers (Fig. 2A–D); bands usually regularly arranged and of equal intensity along palp (Fig. 3A); in some individuals bands more intense and distinct on distal half of palp. Number of bands weakly correlated with total number of chaetigers in an individual (Fig. 3B).

Prostomium with shallow anterior incision often seen only in ventral view, posteriorly extending to end of chaetiger 3 (usually to middle of chaetiger 3) as a low caruncle, shorter in small individuals (Fig. 3C). Short occipital antenna present on caruncle in individuals with more than 90 chaetigers; smaller individuals usually without antenna. Two pairs of black eyes usually present. Palps as long as 15–30 chaetigers, with longitudinal frontal groove lined with fine cilia, latero-frontal motile compound cilia, and papillae with short non-motile cilia densely arranged in 4–5 rows along both sides of frontal groove (Fig. 2C), and also sparsely scattered on lateral and abfrontal palp surfaces all along palp length (Fig. 2D).

Chaetiger 1 with short capillaries in neuropodia and small postchaetal lamellae in both rami; notochaetae absent. Notopodia of posterior chaetigers with two kinds of heavy spines in addition to 2–6 slender capillaries (Fig. 2H). One spine slender and slightly curved, awl-like (Fig. 2H, *sl*), second spine heavily recurved, sickle-shaped (Fig. 2H, *he*); spines with curved tips directed medially. Slender awl-like spines first appearing in chaetiger 18 in juveniles with 18–19 chaetigers, while heavy sickle-shaped spines first appearing in notopodia in juveniles with 25–30 chaetigers (Table 1: 25-chaetiger individual). Both kinds of spines beginning from more posterior chaetigers in larger individuals (Fig. 3D) what can only be explained by their falling out from anterior notopodia with growth of worms. Slender awl-like spines and heavy sickle-shaped spines developing and falling out at different rates and, therefore, arranged in notopodia differently (Table 1). In notopodia of new segments developing in growth zone in front of pygidium in worms with more than 25 chaetigers, capillaries and heavy sickle-shaped spines developing first while slender awl-like spines developing later. Consequently, notopodia of a few posteriormost chaetigers bearing only capillaries and heavy sickle-shaped spines. With growth, heavy sickle-shaped spines of anteriormost spine-bearing notopodia falling out first while slender awl-like spines falling out gradually afterwards. Consequently, notopodia of a few anteriormost chaetigers bearing only capillaries and slender awl-like spines. Middle spine-bearing notopodia having both kinds of spines in addition to capillaries. Anterior position of spines correlated with arrangement of branchiae (Table 1). In small individuals, spines first present from 4–17 chaetigers after last branchiate chaetiger. In mid-size individuals, slender awl-like spines usually from last branchiate chaetiger and heavy sickle-shaped spines usually beginning 1–3 chaetigers after last branchiate chaetiger. In large individuals, slender awl-like spines usually from 1–3 chaetigers before last branchiate chaetiger, while heavy sickle-shaped spines usually beginning in last branchiate chaetiger or in next chaetiger after it.

Chaetiger 5 twice as large as chaetigers 4 and 6, with up to six dorsal superior winged capillaries, seven heavy falcate spines arranged in a slightly curved diagonal row and alternating with bilimbate-tipped companion chaetae, and seven ventral winged capillaries. Dorsal superior and ventral capillaries shorter and fewer than those on adjacent chaetigers. Falcate spines with large subdistal flange on lateral side; upper and inner parts of flange thinner than lower and outer parts, thus in newly developed spines (situated in posterior part of spine row) whole structure appearing as a large tooth joined to main fang by thin sheath; in older spines (situated in anterior part of spine row) lateral flange greatly worn and indistinct.

Hooks in neuropodia from chaetiger 7, up to 12 in a series, not accompanied by capillaries. Hooks bidentate; shaft slightly curved, with weak constriction in upper part (Fig. 2G).

Branchiae from chaetiger 7, full-sized from chaetigers 10–12, gradually diminishing in size along posterior half of body, absent on 5–20 posteriormost chaetigers (Fig. 3D). Branchiae flattened, with surfaces oriented parallel to body axis, free from notopodial postchaetal lamellae, with longitudinal row of cilia along inner surface.

Nototrochs from chaetigers 7–8 onwards, each composed of one row of short cilia, on branchiate chaetigers extending onto branchiae.

Pygidium disk-like to cup-shaped, usually with distinct dorsal gap, white due to numerous striated glandular cells (Fig. 2F).

Glandular pouches in neuropodia from chaetiger 6 in individuals with up to about 30 chaetigers, from chaetiger 7 in larger individuals; pouches large in chaetigers 7–9 and considerably smaller in successive chaetigers.

Digestive tract without ventral buccal bulb and gizzard-like structure.

Nephridia from chaetiger 7 onwards, greenish in life; pairs of nephridia on each chaetiger opening to exterior middorsally via two closely situated nephridiopores.

Habitat. Adults of *P. hoplura* make U-shaped burrows in shells of barnacles, various gastropods and bivalves, including abalone and oysters. Worm burrows appear as detrital tubes inside shells: the walls of the burrows are lined with detritus, and median space of each burrow is also filled with detritus forming a medial wall. Each burrow opens to the outside via two joined apertures forming a characteristic 8-shaped hollow in a shell, and extended by two smooth silty tubes each up to 5 mm long.

In Italy and France, adults of *P. hoplura* were found in shells of live whelk *Stramonita haemastoma*, European flat oyster *Ostrea edulis*, Pacific oyster *Crassostrea gigas*, empty shells of pilgrim scallop *Pecten maximus* (Linnaeus, 1758), and empty shell of gastropod *Ocenebra erinaceus* occupied by hermit crab *Clibanarius erythropus*. The worms were rare and did not cause serious damage to the mollusks.

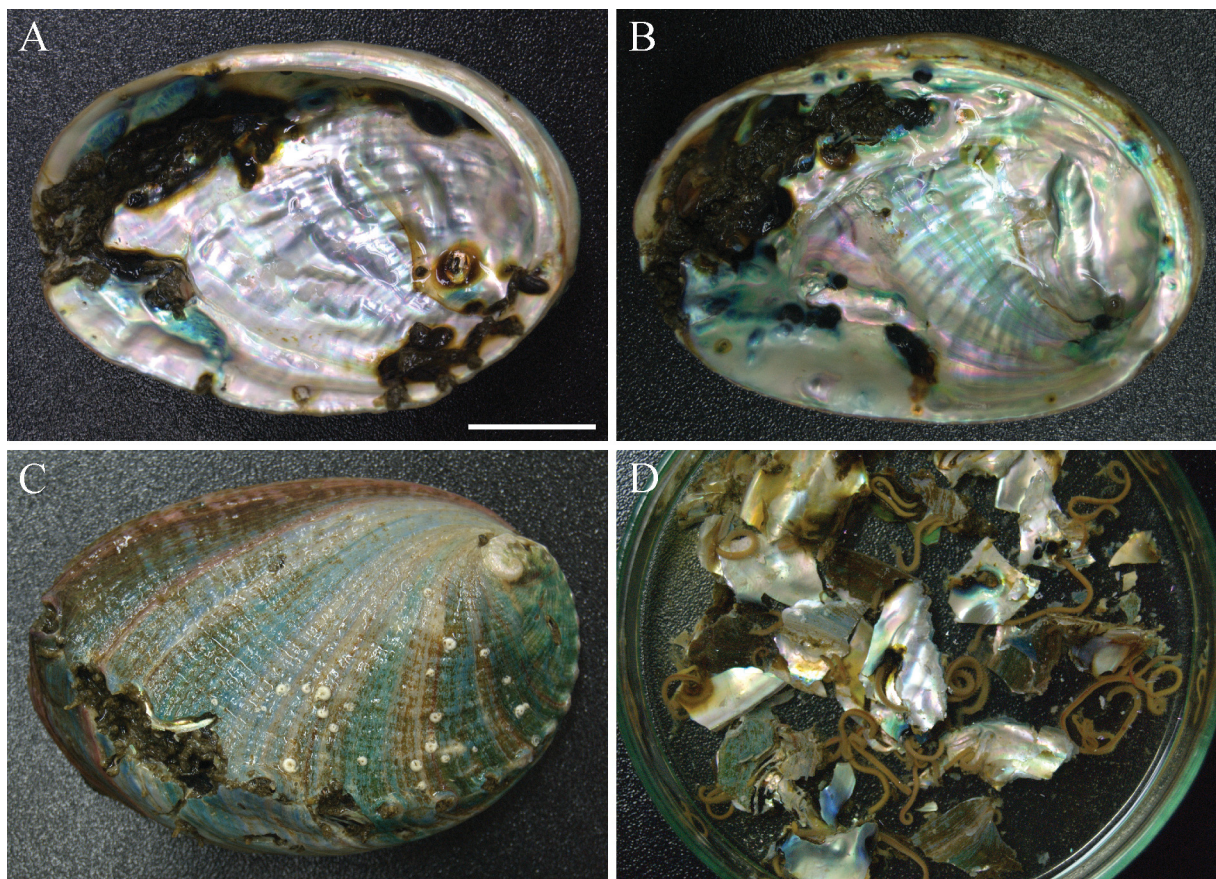


FIGURE 4. Shells of abalone *Haliotis discus hannai* cultivated in land-based tanks and severely infested by *Polydora hoplura* (Jeju Is., South Korea. MIMB 28076). A, B, inner surface of shells showing respiratory holes of the mollusks clogged by *Polydora hoplura*. C, same, outer surface of shell. D, one abalone shell broken into pieces, showing severe infestation by about 80 individuals of *Polydora hoplura*. Scale bar for all = 2 cm.

TABLE 1. Usual arrangement of branchiae, slender awl-like spines and heavy sickle-shaped spines in 17 posterior chaetigers of different size individuals of *P. hoplura*.

25-chaetiger individual				50-chaetiger individual			
chaetiger	branchia	awl-like spine	sickle-like spine	chaetiger	branchia	awl-like spine	sickle-like spine
9	+			34	+		
10	+			35	+		
11	+			36	+		
12	+			37	+		
13	+			38	+		
14				39	+		
15				40	+		
16				41			
17				42		+	
18		+		43		+	
19		+		44		+	+
20		+		45		+	+
21		+		46		+	+
22		+		47			+
23		+		48			+
24		+		49			+
25		+		50			+
pygidium				pygidium			

continued.

100-chaetiger individual				150-chaetiger individual			
chaetiger	branchia	awl-like spine	sickle-like spine	chaetiger	branchia	awl-like spine	sickle-like spine
84	+			134	+		
85	+			135	+	+	
86	+	+		136	+	+	
87	+	+		137	+	+	
88		+		138		+	+
89		+	+	139			+
90		+	+	140			+
91			+	141			+
92			+	142			+
93			+	143			+
94			+	144			+
95			+	145			+
96			+	146			+
97			+	147			+
98			+	148			+
99			+	149			+
100			+	150			+
pygidium				pygidium			

In South Korea, *P. uncinata* (= *P. hoplura*) was first recorded in 2004 from the oysters cultivated in Geoje and Goseong (south-eastern part of South Korea), but not found in abalone cultivated in sea cages (Sato-Okoshi *et al.* 2012). In the present study, we found up to three worms per shell in abalone cultivated in cages in the sea in Wando county, and a maximum of 80 large worms in one shell of abalone cultivated in land-based tanks on Jeju Island (Fig. 4D). In many cases worms caused formation of dark brown muddy or nacreous, parchment-like blisters on the inner shell surface (Fig. 4A–C). Heavy infestation by *P. hoplura* occasionally caused secondary bacterial infestation, clogging of respiratory pores and death of mollusk. In contrast to abalone, shells of the Pacific oyster *C. gigas* widely cultivated around Geoje Island were rarely infested by *P. hoplura* which seems to not effect oyster condition.

Discussion

Adult worms from France and South Korea examined in the present study appear similar to those from Italy and are referred to the same species, *P. hoplura*. Earlier, Radashevsky & Migotto (2016) for the first time described worms of the same morphology from São Paulo, Brazil, and California, USA, and showed that *P. uncinata* originally described from Japan by Sato-Okoshi (1998) was identical with *P. hoplura* from the type locality in Italy. Sato-Okoshi *et al.* (2016) showed *P. uncinata* from Japan and Australia and *P. hoplura* from South Africa were not genetically different (based on 16S, 18S, 28S rRNA and *cyt b* sequences) and the worms exhibited great overlap in morphology. Thus, they recommended synonymization of the two species.

The original and most later descriptions of *P. hoplura* from European waters identified the recurved spines in posterior notopodia as a major diagnostic character of the species but did not mention pigment bands on the palps and the occipital antenna on the caruncle of larger specimens. Because of this, *Boccardiella hamata* (Webster, 1879) was erroneously treated as a junior synonym of *P. hoplura* (e.g., Carazzi 1893), and the sponge-boring *Polydora colonia* Moore, 1907 worms were likely misidentified as *P. hoplura* by some authors (e.g., Southern 1914; Rioja 1917b; Southward 1956); both *B. hamata* and *P. colonia* adults have recurved spines in posterior notopodia as in *P. hoplura*.

Carazzi (1893) and Lo Bianco (1893) reported transverse brown bands on palps in Italian specimens and Read (1975) was the first to report a low occipital antenna in the specimens from New Zealand. Variably developed dark bands on palps, the occipital antenna, and the caruncle extending to almost end of chaetiger 3 were observed in specimens from the Gulf of Naples, Italy, examined in the present study. These features, in addition to the recurved spines in posterior notopodia, constitute a unique set of adult morphological characters to distinguish *P. hoplura* from closely related species. These characters were confirmed by earlier authors in individuals from South Africa, New Zealand, Australia and Japan, thus supporting conspecificity of their specimens with *P. hoplura* from Italy. It should be noted that the first three characters are size-dependent and appear some time after settlement and metamorphosis of an individual.

Patchy distribution of *P. hoplura* around the world (Fig. 1) has likely been the result of unintentional transportations of worms through various human activities, mainly abalone and oysters aquaculture. The worms were likely introduced from Brittany, France into Dutch waters with imported oysters used to replenish depleted stocks (Korringa 1951). They were transported with abalone brood stock from Japan to Chile (Radashevsky & Olivares 2005, as *P. uncinata*), and also probably introduced into South Africa (Mead *et al.* 2011).

Although *P. hoplura* has been known in Europe for almost 150 years and only recently reported from Asian waters (as *P. uncinata*), its native distribution and place of origin remain uncertain. The species may have originated in Europe but is also possible that the worms were introduced with the Portuguese oyster *C. angulata* Lamarck, 1819 transported by Portuguese, Spanish or Dutch sailors from Asia at least four centuries ago (Boudry *et al.* 1998; Lapègue *et al.* 2004; Wang *et al.* 2010). As such, *P. hoplura* is likely a cryptogenic species in European waters with actual place of origin unknown. The conspecificity of distant populations of *P. hoplura* requires genetic confirmation while the native distribution and vectors of transportation of the species across the world need a large-scale population analysis.

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